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RESEARCH ARTICLE

Phylogeny of the Neotropical longhorn beetle genus *Ateralphus* (Coleoptera: Cerambycidae: Lamiinae)

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ABSTRACT. *Ateralphus* Restello, Iannuzzi & Marinoni, 2001 is a Neotropical genus of longhorn beetles composed of nine species. This genus was proposed from splitting *Alphus* White, 1855 into other two genera: *Ateralphus* and *Exalphus* Restello, Iannuzzi & Marinoni, 2001. Even though *Ateralphus* (nine species), *Alphus* (four) and *Exalphus* (18) were recently revised, their validity has not been tested using phylogenetic methods. In this study, we carried out a cladistic analysis of *Ateralphus* and its related genera, *Alphus* and *Exalphus*, based on 44 morphological characters of the adults, to test their monophyly and infer the relationships between their species. Our results support the monophyly of the three genera and recovered two clades that corroborate the species-groups previously recognized in *Ateralphus*. A new genus, *Grandateralphus* **gen. n.**, is proposed for one of these clades, which is supported by three synapomorphies: width of upper ocular lobes less than width between the lobe and the coronal suture (character state 6: 0), genae parallel in frontal view (8: 1) and scape gradually expanded toward apex, reaching widest diameter just near apex (9: 2). *Grandateralphus* **gen. n.** includes three new combinations: *G. lacteus* (Galileo & Martins, 2006), **comb. n.**; *G. tumidus* (Souza & Monné, 2013), **comb. n.**; and *G. variegatus* (Mendes, 1938), **comb. n.** Notes on the distribution of *G. variegatus* **comb. n.** and a new record of *E. cicatricornis* Schmid, 2014 for Bolivia (Santa Cruz) are provided.

KEY WORDS. Acanthoderini, cladistics, distribution, new combination, taxonomy.

INTRODUCTION

Ateralphus Restello, Iannuzzi & Marinoni, 2001 is a Neotropical genus of longhorn beetles belonging to Acanthoderini, a tribe of Lamiinae described by Thomson (1860). The tribe Acanthoderini includes 553 species classified into 67 genera, according to Tavakilian and Chevillotte (2016), and is characterized mainly by the piriform scape, shorter than antennomere III, and by the spines or lateral tubercles of the prothorax. Originally, *Ateralphus* species were classified in *Alphus*, a genus described by White (1855) for five species, including *Alphus subsellatus* White, 1855 (subsequently designated as type-species of *Ateralphus* by Restello et al. (2001)). Restello et al. (2001) proposed two additional genera for species previously included in *Alphus* White, 1855: *Ateralphus* and *Exalphus*; and summarized, in a table, the main characteristics to differentiate the three genera from one another. As part of that contribution, 15 species were included in *Exalphus* (13 new combinations and two new species), six new combinations were proposed for *Ateralphus*, and only three species were kept in *Alphus*.

All species of *Alphus* and *Ateralphus* are distributed in South America. Most of them occur in dense forests, such as the Atlantic and the Amazon forests. There are only a few records from open biomes such as the Cerrado and Chaco for *Ateralphus subsellatus* (White, 1855) and *Ateralphus dejeani* (Lane, 1973). *Exalphus*, in contrast, has a broader distribution, from Guatemala to south of South America, with only one species occurring in Central America (*Exalphus cavifrons* (Bates, 1872)).

Recently, *Alphus* (four species) and *Exalphus* (18) were studied by Souza and Monné (2013a) and Souza and Monné (2014), respectively, who updated the distribution data and provided an identification key for their species. After Souza and Monné (2014), two new species were described in *Exalphus*: *E. docquini* Tavakilian & Néouze, 2013 and *E. cicatricornis* Schmid,

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2014. *Ateralphus* (nine species) was revised by Souza and Monné (2013b). They recognized two groups of species in the genus, but failed to name them. In the first group, characterized mainly by the upper ocular lobes separated by three or more times their width, lower ocular lobes narrow and rectangular-shaped, genae parallel to divergent and tibiae with one ring or spot of dark brown setae on sub-apical region, they included *A. lacteus* Galileo & Martins, 2006, *A. tumidus* Souza & Monné, 2013 and *A. variegatus* (Mendes, 1938). In the second group, characterized by the upper ocular lobes separated by less than or equal to twice their width, lower ocular lobes large and rounded, genae convergent and tibiae with dense ring of dark brown setae on apical region, they included the other species of the genus.

In Cerambycidae, new taxa are frequently proposed based only on descriptive taxonomy. In this contribution, we evaluate whether the split of *Ateralphus* and *Exalphus* from *Alphus*, proposed by Restello et al. (2001), can be corroborated through cladistic methods. Our specific goals are: (1) to test the monophyly of *Ateralphus* and its related genera (*Alphus* and *Exalphus*) through phylogenetic analysis based on morphological characters; and (2) to evaluate whether the species groups mentioned by Souza and Monné (2013b) for *Ateralphus* may be corroborated and formalized as autonomous genera. Additionally, notes on the taxonomy and distribution of some species are provided.

MATERIAL AND METHODS

Taxon sampling

We included in the phylogenetic analysis all species currently classified in *Ateralphus*, *Alphus* and 15 of the 18 species placed in *Exalphus*. *Exalphus simplex* (Galileo & Martins, 1998), *E. vicinus* Galileo & Martins, 2003 and *E. docquini* were not included in this study because we were not able to obtain specimens for examination. Since there are no previous phylogenetic studies on the Acanthoderini, we chose our outgroups from species which had been considered close to the ingroup taxa, *Alphus*, *Ateralphus* and *Exalphus*, in previous taxonomic treatments (i.e., Bates (1862), Lacordaire (1872), Martins (1985) and Martins and Galileo (2007)). Additionally, we also selected some representatives of Acanthoderini that bear some morphological resemblance to the species of the ingroup. Therefore, the following species were chosen as outgroups: *Cotyzineus bruchi* (Melzer, 1931), *Myoxinus pictus* (Erichson, 1847), *Nesozineus alphoides* (Lane, 1977) and *Acanthoderes albitarsis* Laporte, 1840, which was used to root the tree in our analysis. In total, 32 terminal taxa were included in the cladistics analysis, comprising 28 ingroup species and four outgroup species (Table 1).

Characters and analysis procedures

The characters were constructed from the external morphology of the adults and male genitalia. Several are modified from previous taxonomic studies on the ingroup species, such as Bates (1862), Restello et al. (2001) and Souza and Monné (2013b). In total, 44 characters were included in the analysis (27 binary and 17 multistate). The description of the characters and their states follows the structural concepts proposed by Sereno (2007). In the matrix, missing data is indicated by '?'. The characters and their respective states are listed below, and the data matrix is in Table 1. Following the description of each character, in the list of characters, we provide the length (L), consistency index (CI) and retention index (RI) based on the selected most parsimonious topology.

All characters were treated as unordered (or non-additive) and equally weighted. The search for the most parsimonious topologies was conducted in WinClada version 1.00.08 (Nixon 1999–2002), through NONA version 2.0 (Goloboff 1993), using the following commands: number of replications (mult*N) = 1000; starting tree per replication (hold/) = 10; random seed = 1; Multiple TBR + TBR (mult*max*). The character transformations presented on the selected topology are either unambiguous changes or were optimized under fast optimization (ACCTRAN). Branch supports values were calculated in TNT (version 1.1, [August, 2011], Goloboff et al. 2008). Bootstrap values were calculated from an independent analysis using 1000 pseudoreplicates and Bremer support (Bremer 1994) was calculated based on the strict consensus topology using 1000 suboptimal trees up to one step longer.

List of characters

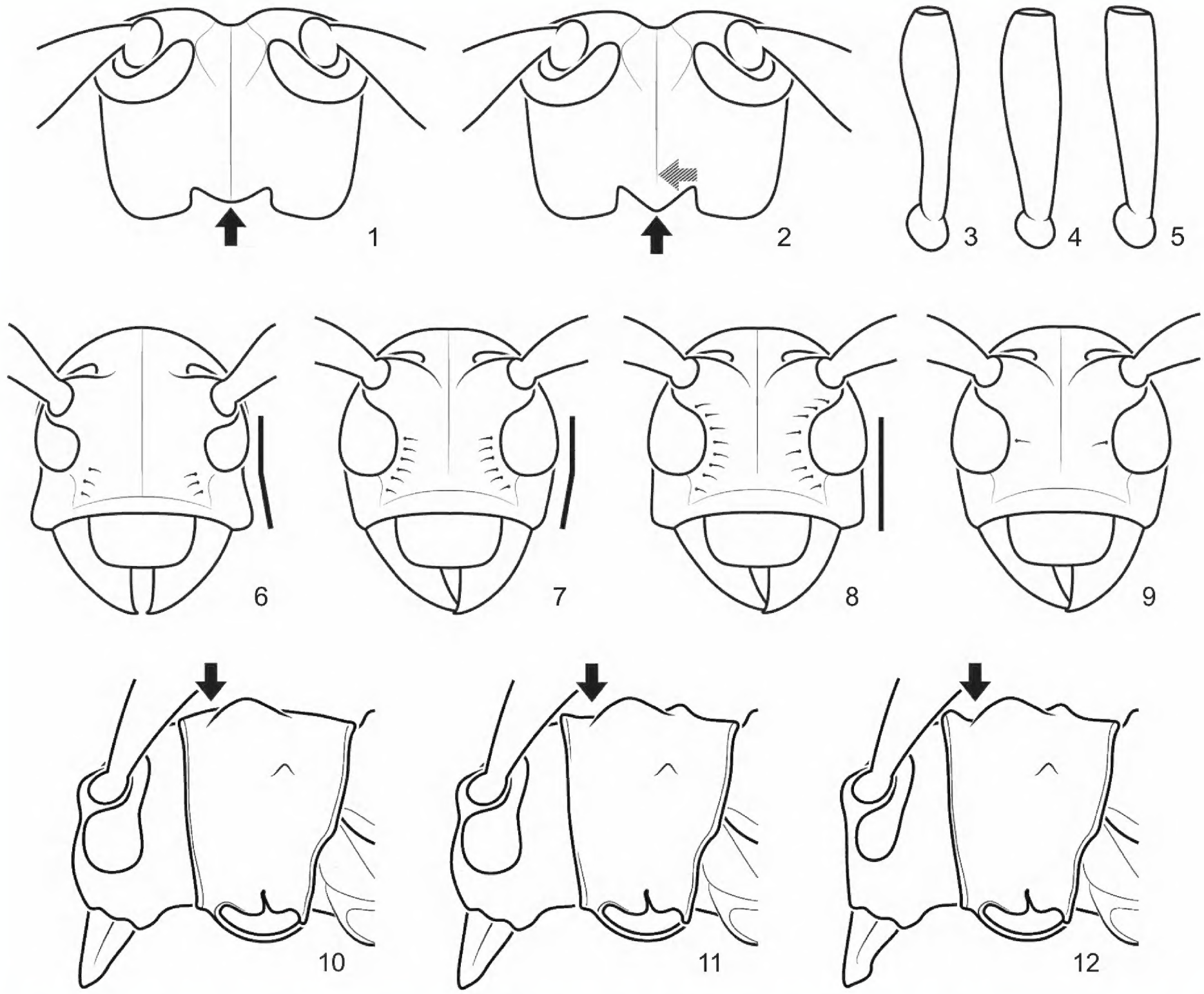
1. Head, posterior margin, shape: (0) rounded (Fig. 1); (1) triangular (Fig. 2). L = 2; CI = 50; RI = 92.
2. Head, coronal suture, relative to posterior margin: (0) not reaching (Fig. 2); (1) reaching (Fig. 1). L = 2; CI = 50; RI = 88.
3. Head, erect setae on base of antennal tubercles: (0) absent; (1) present. L = 1; CI = 100; RI = 100.
4. Head, coarse punctation between upper ocular lobes: (0) absent; (1) present. L = 4; CI = 25; RI = 76.
5. Frons, erect setae near the genal suture: (0) a row reaching the base of the lower ocular lobes (Fig. 6); (1) a row reaching approximately basal half of the antennal tubercles (Fig. 7); (2) a row reaching antennal tubercles (Fig. 8); (3) only one seta at half of the lower ocular lobes (Fig. 9). L = 4; CI = 75; RI = 90.
6. Upper ocular lobes (U), width relative to the width from lobe to coronal suture (W): (0) U less than W; (1) U subequal to W; (2) U larger than W. L = 9; CI = 22; RI = 50.
7. Lower ocular lobes (L), height relative to gena (G): (0) L less than G; (1) L subequal to G; (2) L larger than G. L = 3; CI = 66; RI = 83.
8. Genae, shape, in frontal view: (0) divergent toward apex (Fig. 6); (1) parallel (Fig. 8); (2) convergent toward apex (Fig. 7). L = 4; CI = 50; RI = 83.
9. Antennae, scape, shape: (0) piriform (Fig. 3); (1) gradually expanded toward apex, reaching widest diameter at one third from apex (Fig. 4) (2) gradually expanded toward

Table 1. Data matrix of morphological characters used in the cladistic analysis of *Ateralphus* and related genera, *Alphus* and *Exalphus* (Coleoptera: Cerambycidae: Lamiinae). Outgroups are indicated with an asterisk.

Taxa	Characters																																											
	0									1										2										3										4				
	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4
*Acanthoderes albitarsis**	1	0	0	0	0	0	0	0	0	0	2	2	0	1	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	1	1	1	0	0
Alphus capixaba	0	0	0	1	1	2	2	2	1	0	0	1	0	0	2	1	0	1	1	0	0	0	1	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	?	?	?	?
Alphus marinonii	0	0	0	0	1	2	2	2	1	0	0	0	0	0	2	1	0	1	1	1	0	0	1	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	?	?	?	?
Alphus similis	0	0	0	0	1	1	2	2	1	0	0	1	0	0	2	1	0	1	1	1	0	0	1	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	1	0	1
Alphus tuberosus	0	0	0	0	1	2	2	2	1	0	0	0	0	0	2	1	0	1	1	1	0	0	1	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	1	0	1
Ateralphus auritarsus	0	1	0	0	1	1	1	2	1	0	1	2	0	1	0	0	1	2	0	0	0	1	1	0	0	0	0	1	0	1	0	0	0	0	0	1	0	1	0	1	?	?	?	?
Ateralphus dejeani	0	1	0	0	1	1	2	2	1	0	1	2	0	1	0	0	1	2	0	0	0	1	1	0	1	0	0	1	0	1	1	0	1	0	0	1	0	1	0	1	1	1	0	0
Ateralphus javariensis	0	1	0	0	1	2	2	2	1	0	1	2	0	1	0	0	1	2	0	0	0	1	1	0	0	0	0	1	0	1	1	0	1	0	0	1	0	1	0	1	?	?	?	?
Ateralphus lacteus	0	1	0	0	1	0	1	1	2	0	1	2	0	1	0	0	1	0	0	0	0	1	1	0	0	0	0	1	0	0	0	0	0	0	0	2	0	1	0	1	1	1	1	0
Ateralphus lucianeae	0	1	0	0	1	1	2	2	1	0	1	2	0	1	0	0	1	2	0	0	0	1	1	0	1	0	0	1	0	1	1	0	1	0	0	1	0	1	0	1	?	?	?	?
Ateralphus senilis	0	1	0	0	1	2	2	2	1	0	1	2	0	1	0	0	1	2	0	0	0	1	1	0	1	0	0	1	0	1	1	0	1	0	0	1	0	1	0	1	1	1	0	0
Ateralphus subsellatus	0	1	0	0	1	1	1	2	1	0	1	2	0	1	0	0	1	2	0	0	0	1	1	0	0	0	0	1	0	1	0	0	0	0	0	1	0	1	0	1	1	1	0	0
Ateralphus tumidus	0	1	0	0	1	0	1	1	2	0	1	2	0	1	0	0	1	0	0	0	0	2	1	0	0	0	0	1	0	0	0	0	0	0	0	2	1	1	1	1	1	1	0	0
Ateralphus variegatus	0	1	0	0	1	0	1	1	2	0	1	2	0	1	0	0	1	0	0	0	0	1	1	0	0	0	0	1	0	0	0	0	0	0	0	2	0	1	1	1	1	1	1	0
*Cotyzineus bruchi**	0	0	0	0	3	1	1	2	1	0	0	1	0	1	0	1	1	1	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	1	1	0	0
Exalphus aurivillii	?	?	0	1	2	2	2	2	1	0	0	2	1	1	1	2	1	1	1	0	1	1	0	1	0	0	1	0	1	0	0	2	0	0	1	2	1	1	0	0	?	?	?	?
Exalphus biannulatus	1	0	0	1	2	2	2	1	1	0	0	2	1	1	1	2	1	1	1	1	0	1	0	1	0	0	1	0	1	0	0	2	0	0	1	2	1	1	0	0	1	1	0	0
Exalphus calvifrons	1	0	1	0	2	2	2	1	2	0	0	1	0	1	1	2	1	1	1	1	0	1	0	1	0	0	1	0	1	0	0	1	0	0	1	2	1	1	0	0	2	1	2	0
Exalphus cicatricornis	?	?	1	0	2	2	2	1	2	1	0	1	0	1	1	2	1	1	1	1	0	1	0	1	0	0	1	0	1	0	0	1	0	0	1	2	1	1	0	?	?	?	?	?
Exalphus colasi	1	0	0	1	2	1	2	2	1	0	0	1	1	1	1	2	1	1	1	1	1	1	0	1	1	0	1	1	1	0	0	2	0	0	1	2	1	1	0	0	1	0	0	0
Exalphus confusus	1	0	0	1	1	1	2	2	1	0	0	1	0	1	1	1	1	1	1	0	1	1	0	1	0	0	1	0	0	0	0	2	0	0	1	2	1	1	0	0	1	2	0	0
Exalphus foveatus	1	0	0	1	1	2	2	2	1	0	0	1	0	1	1	1	1	1	1	0	1	1	0	1	0	0	1	0	0	0	0	2	0	0	1	2	1	1	0	0	1	2	0	0
Exalphus gounellei	1	0	0	1	1	2	2	1	1	0	0	1	1	1	1	2	1	1	1	0	0	1	0	1	0	0	1	0	1	0	0	1	0	0	1	2	1	1	0	0	1	2	0	0
Exalphus guaraniticus	1	0	1	1	2	1	2	1	1	0	0	1	1	1	1	2	1	1	1	1	0	1	0	1	0	0	1	0	1	0	0	1	0	0	1	2	1	1	0	0	3	1	0	0
Exalphus leuconotus	1	0	1	1	2	1	2	1	1	0	0	1	1	1	1	2	1	1	1	1	0	1	0	1	0	0	1	0	1	0	0	1	0	0	1	2	1	1	0	0	3	1	0	0
Exalphus lichenophorus	1	0	1	1	2	2	2	1	2	0	0	1	1	1	1	2	1	1	1	1	0	1	0	1	0	0	1	0	1	0	0	1	0	0	1	2	1	1	0	0	?	?	?	?
Exalphus malleri	1	0	1	0	2	2	2	1	2	1	0	1	1	1	1	2	1	1	1	1	0	1	0	1	0	0	1	0	1	0	0	1	0	0	1	2	1	1	0	0	1	1	0	0
Exalphus solangeae	?	?	0	1	1	1	2	1	1	0	?	?	1	1	1	2	1	1	1	1	1	1	0	1	0	0	1	0	0	0	0	2	0	0	1	2	1	1	0	0	?	?	?	?
Exalphus spilonotus	1	0	0	1	1	2	2	2	1	0	0	1	0	1	1	1	1	1	1	1	0	1	1	1	0	0	0	0	1	0	0	2	0	0	1	2	1	1	0	0	3	2	0	0
Exalphus zellibori	1	0	0	1	2	1	2	2	1	0	0	1	1	1	1	2	1	1	1	1	1	1	0	1	1	0	1	1	1	0	0	2	0	0	1	2	1	1	0	0	1	1	0	0
*Myoxinus pictus**	1	0	0	1	0	2	1	0	1	0	2	2	1	1	1	1	1	0	0	0	0	1	0	0	0	0	1	0	1	0	0	0	0	0	1	2	0	0	0	0	1	2	0	0
*Nesozineus alphoides**	0	1	0	0	1	2	2	2	1	0	0	1	0	0	0	1	1	1	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0

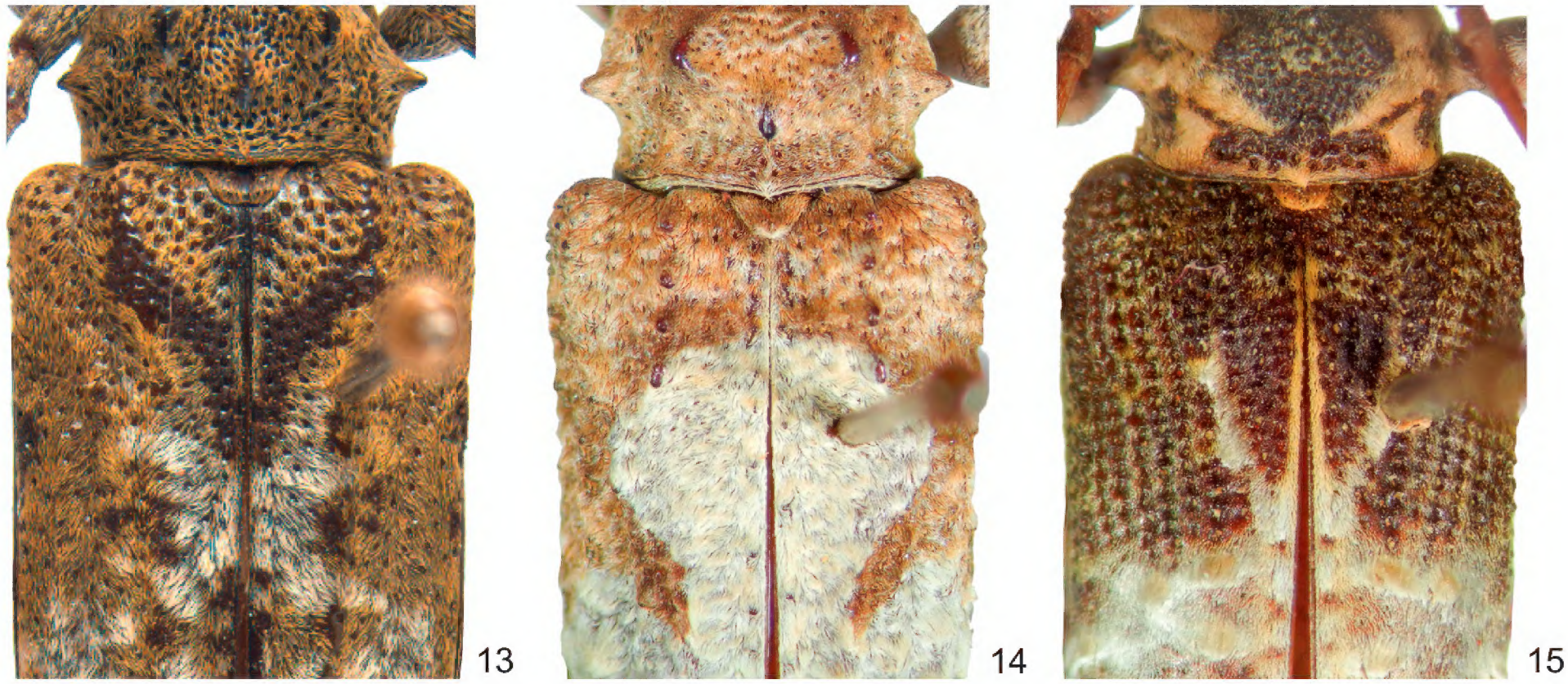
apex, reaching widest diameter near the apex (Fig. 5). L = 3; CI = 66; RI = 83.

10. Antennae, scape, scar at outer surface of apex: (0) absent; (1) present. L = 2; CI = 50; RI = 0.
11. Antennae, antennomere III, length relative to antennomere IV: (0) III shorter than IV; (1) III subequal to IV; (2) III longer than IV. L = 2; CI = 100; RI = 100.
12. Antennae, antennomere III, length relative to antennomere V: (0) III shorter than V; (1) III subequal to V; (2) III longer than V. L = 4; CI = 50; RI = 84.
13. Antennae, antennomeres III to XI, stain of dark brown setae on half basal region: (0) absent; (1) present. L = 3; CI = 33; RI = 80.
14. Antennae, antennomeres III to XI, stain of dark brown setae on apical region: (0) absent; (1) present. L = 1; CI = 100; RI = 100.
15. Prothorax, coverage pattern of setae: (0) uniformly covered by same color and density setae; (1) with a denser line of white setae at median region; (2) with denser distinct stains of white setae near the lateral tubercle. L = 3; CI = 66; RI = 92.
16. Pronotum, anterior margin, shape: (0) straight (Fig. 10); (1) slightly depressed (Fig. 11); (2) deeply depressed (Fig. 12). L = 3; CI = 66; RI = 94.
17. Pronotum, midline, glabrous tubercle or elevation: (0) absent; (1) present. L = 1; CI = 100; RI = 100.
18. Pronotum, elevation post-lateral to median tubercles: (0) absent; (1) slightly elevated, inconspicuous; (2) distinctly elevated, as a pair of tubercles. L = 2; CI = 100; RI = 100.
19. Pronotum, longitudinal elevation from pair of median tubercles toward posterior margin: (0) absent; (1) present. L = 1; CI = 100; RI = 100.



Figures 1–12. Schematic representation of the character states used in the cladistics analysis of *Ateralphus* and related genera, *Alphus* and *Exalphus*. 1–2, head in dorsal view: 1, *Ateralphus subsellatus*, posterior margin rounded (1:0; black arrow) and coronal suture reaching posterior margin (2:1); 2, *Exalphus leuconotus* (Thomson, 1860), posterior margin triangular (1:1; black arrow) and coronal suture reaching posterior margin (2:0; striped arrow). 3–5, shape of scape: C3, *A. albitarsis*, scape piriform (9:0); 4, *A. subsellatus*, scape gradually expanded toward apex, reaching the widest diameter at one third from apex (9:1); 5, *Ateralphus variegatus*, scape gradually expanded toward apex, reaching the widest diameter near the apex (9:2). 6–9, head in frontal view: 6, *A. albitarsis*, row of setae reaching the base of the lower ocular lobes (5:0) and genae divergent toward apex (8:0); 7, *A. subsellatus*, row of setae reaching the basal half of the antennal tubercles (5:1) and genae convergent toward apex (8:2); 8, *E. leuconotus*, row of setae reaching the antennal tubercles (5:2) and genae parallel (8:1); 9, *Cotyzineus bruchi*, only one seta at half of the lower ocular lobes (5:3). 10–12, prothorax in lateral view (character states are indicated by black arrow): 10, *Alphus tuberosus* (Germar, 1824), pronotum straight near anterior margin (16:0); 11, *A. subsellatus*, pronotum slight depressed near anterior margin (16:1); 12, *E. leuconotus*, pronotum deeply depressed near anterior margin (16:0).

20. Prosternal process, lateral margins, shape: (0) straight; (1) with a prominence at post-median region. L = 5; CI = 20; RI = 69.
21. Mesosternal process (Mp), length relative to mesocoxa (Mc): (0) Mp shorter than Mc; (1) Mp subequal to Mc; (2) Mp larger than Mc. L = 2; CI = 50; RI = 80.
22. Mesosternal process, shape: (0) slightly convex; (1) straight; (2) tumescent. L = 2; CI = 100; RI = 100.
23. Mesosternal process, approximated angle at the apical third relative to mesosternum: (0) 90°; (1) 45°; L = 2; CI = 50; RI = 93.



Figures 13–15. Punctures on basal third of the elytra (character 20) observed among the species included in the cladistic analysis. 13–14, Punctures irregularly distributed, represented by *Ateralphus subsellatus* and *Exalphus leuconotus*, respectively; 15, punctures arranged in longitudinal rows, represented by *Alphus tuberosus*.

24. Meso- and metasternum (males), ventral surface, sexual setae: (0) absent; (1) present. L = 1; CI = 100; RI = 100.
25. Scutellum, setae, color pattern: (0) similar to pronotum; (1) covered by dark-brown setae. L = 2; CI = 50; RI = 75.
26. Elytra, basal third, punctures: (0) irregularly distributed (Figs 13, 14); (1) arranged in longitudinal rows (Fig. 15). L = 1; CI = 100; RI = 100.
27. Elytra, basal-crests: (0) absent or slight raised; (1) distinctly raised. L = 2; CI = 50; RI = 92.
28. Elytra, region between basal-crests, setae, color pattern: (0) similar to pronotum; (1) covered by dark-brown setae. L = 2; CI = 50; RI = 90.
29. Elytra, humeral surface: (0) punctate, without raised tubercles; (1) with at least one differentiated and well-developed tubercle at base of humeral carina. L = 3; CI = 33; RI = 83.
30. Elytra, lateral margin, color pattern of setae: (0) with regularly spaced dark-brown stains; (1) similar to the dorsum. L = 1; CI = 100; RI = 100.
31. Femora, basal inner surface, setae, coverage pattern: (0) entirely covered; (1) meso- and/or metafemora glabrous. L = 1; CI = 100; RI = 100.
32. Femora, globose region, setae, coverage pattern: (0) evenly covered with short white setae; (1) mainly covered with sparse white setae, with denser areas forming irregular maculae; (2) mainly covered with sparse white setae, with denser areas forming transverse bands. L = 3; CI = 66; RI = 94.
33. Meso- and metafemora, circular stain of dark brown setae on anterior surface: (0) absent; (1) present. L = 1; CI = 100; RI = 100.
34. Protibiae, shape: (0) straight at base and slight convex toward apex; (1) concave. L = 2; CI = 50; RI = 0.
35. Meso- and metatibiae, half basal region, stain of dark brown setae: (0) absent; (1) present. L = 2; CI = 50; RI = 92.
36. Meso- and metatibiae, apical region, dark brown setae: (0) absent; (1) present. L = 4; CI = 50; RI = 81.
37. Tarsi, tarsomere V, basal third, stain of dark brown setae: (0) absent; (1) present. L = 2; CI = 50; RI = 93.
38. Tarsi, tarsomere V, apical third, stain of dark brown setae: (0) absent; (1) present. L = 2; CI = 50; RI = 85.
39. Abdomen, sternites II-IV, lateral margin, glabrous circular macula: (0) absent; (1) present. L = 1; CI = 100; RI = 100.
40. Sternite V (females), basal region, longitudinal sulcus: (0) absent; (1) present. L = 2; CI = 50; RI = 88.
41. Male genitalia, median lobe, ventral lobe, shape of apex: (0) rounded; (1); truncate; (2) acuminate; (3) with a median salience. L = 4; CI = 75; RI = 50.
42. Male genitalia, median lobe, ventral lobe (V), length relative to dorsal lobe (D): (0) V shorter than D; (1) V subequal to D; (2) V larger than D. L = 6; CI = 33; RI = 20.
43. Male genitalia, tegmen, parameres, distribution pattern of setae: (0) only on apex; (1) on apex and inner margin; (2) on apex and ventral margin. L = 3; CI = 66; RI = 0.
44. Male genitalia, tegmen, basal apophysis, apical region, sclerotization: (0) complete and uniform; (1) with a diagonal line more sclerotized near apex. L = 1; CI = 100; RI = 100.

RESULTS

The cladistic analysis resulted in two most parsimonious cladograms (L = 111, CI = 55 and RI = 86). The cladogram selected (showing unambiguous characters only) to represent the relationships among the taxa is presented in Fig. 16 and a summarized tree with the character states optimized under ACCTRAN optimization is presented in Fig. 17. The monophyly of *Ateralphus*, *Alphus* and *Exalphus* were corroborated in our analysis, with strong branch support values, supporting Restello et al.'s (2001) hypotheses.

The monophyly of *Alphus* was strongly supported in our results by four unambiguous synapomorphies. Three of them are non-homoplastic (Fig. 16), as follows: prothorax with distinct stains of denser setae near the lateral tubercle (character 15: 2); absence of glabrous tubercle or elevation at midline of the

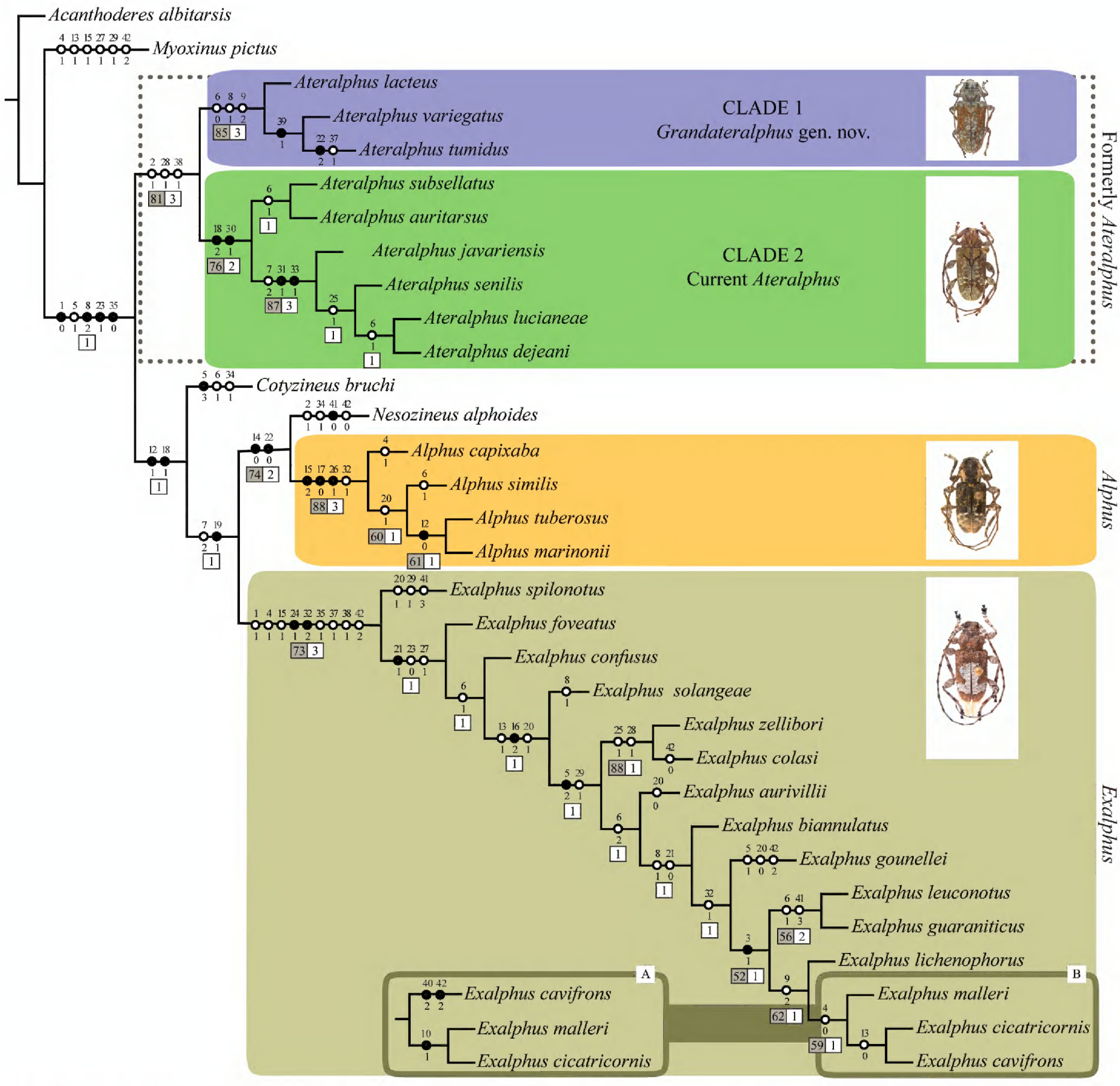


Figure 16. Tree obtained from the cladistics analysis of *Ateralphus* and related genera, *Alphus* and *Exalphus*. Only unambiguous transformations are shown. A and B show the differences between the two most parsimonious topologies. Bootstrap (gray box) and Bremer support (white box) are indicated below each node. Clades are illustrated by the following species: *Alphus similis* Martins, 1985; *Grandateralphus variegatus* comb. n.; *Ateralphus subsellatus*; and *Exalphus leuconotus*.

pronotum (17: 0); and punctures on basal third of the elytra arranged in longitudinal rows (26: 1; Fig. 15). In addition, one homoplastic character also supports this group: the globose region of the femora, mainly covered with sparse white setae, with denser areas forming irregular maculae (32: 1). This state is also present in some apical lineages of *Exalphus*, including *E. calvifrons*, *E. cicatricornis*, *E. gounellei*, *E. guaraniticus*, *E. leuconotus*, *E. lichenophorus* and *E. malleri*. Additionally, one ambiguous, non-homoplastic synapomorphy also corroborates the monophyly of *Alphus* under fast optimization (Fig. 17): basal apophysis with a diagonal line more sclerotized near apex (44: 1).

Exalphus is monophyletic, supported by the following unambiguous synapomorphies (Figs 16, 17): posterior margin of head triangular (1: 1; Fig. 1); presence of coarse punctation between upper ocular lobes (4: 1); prothorax with denser line of white setae at median region (15: 1); males with sexual setae on ventral surface of the meso- and metasternum (24: 1); globose region of femora mainly covered with sparse white setae, with denser areas forming transverse bands (32: 2); meso- and metatibiae with stain of dark brown setae on basal half (35:1); tarsomere V bicolored, with dark brown setae at base and basal third (37: 1); tarsomere V bicolored, with dark brown setae at base and apical third (38: 1); ventral lobe larger than dorsal lobe (42: 2). The character states 24: 1, 32: 2, 37:1 and 38: 1 were first mentioned by Restello et al. (2001) to diagnose *Exalphus* and are confirmed here as synapomorphies for the genus.

Finally, the monophyly of *Ateralphus* was corroborated by three unambiguous, homoplastic synapomorphies (Fig. 16): coronal suture reaching posterior margin of head (2: 1; Fig. 1B); region between basal-crests covered with dark brown setae (28: 1); and tarsomere V with dark brown setae on apical third (38: 1). Additionally, the following three synapomorphies also support the monophyly of *Ateralphus* under fast optimization (Fig. 17): antennomere III subequal to antennomere IV in length (11: 1); pronotum straight near the anterior margin (16: 0); and sternite V with longitudinal sulcus at basal region of the females (40: 1).

Two main clades were obtained in *Ateralphus*, corroborating the species-groups recognized by Souza and Monné (2013b). Clade 1, which includes *A. lacteus*, *A. tumidus* and *A. variegatus*, was supported by the following homoplastic synapomorphies: width of upper ocular lobes less than width between the lobe and the coronal suture (6: 0); genae parallel in frontal view (8:

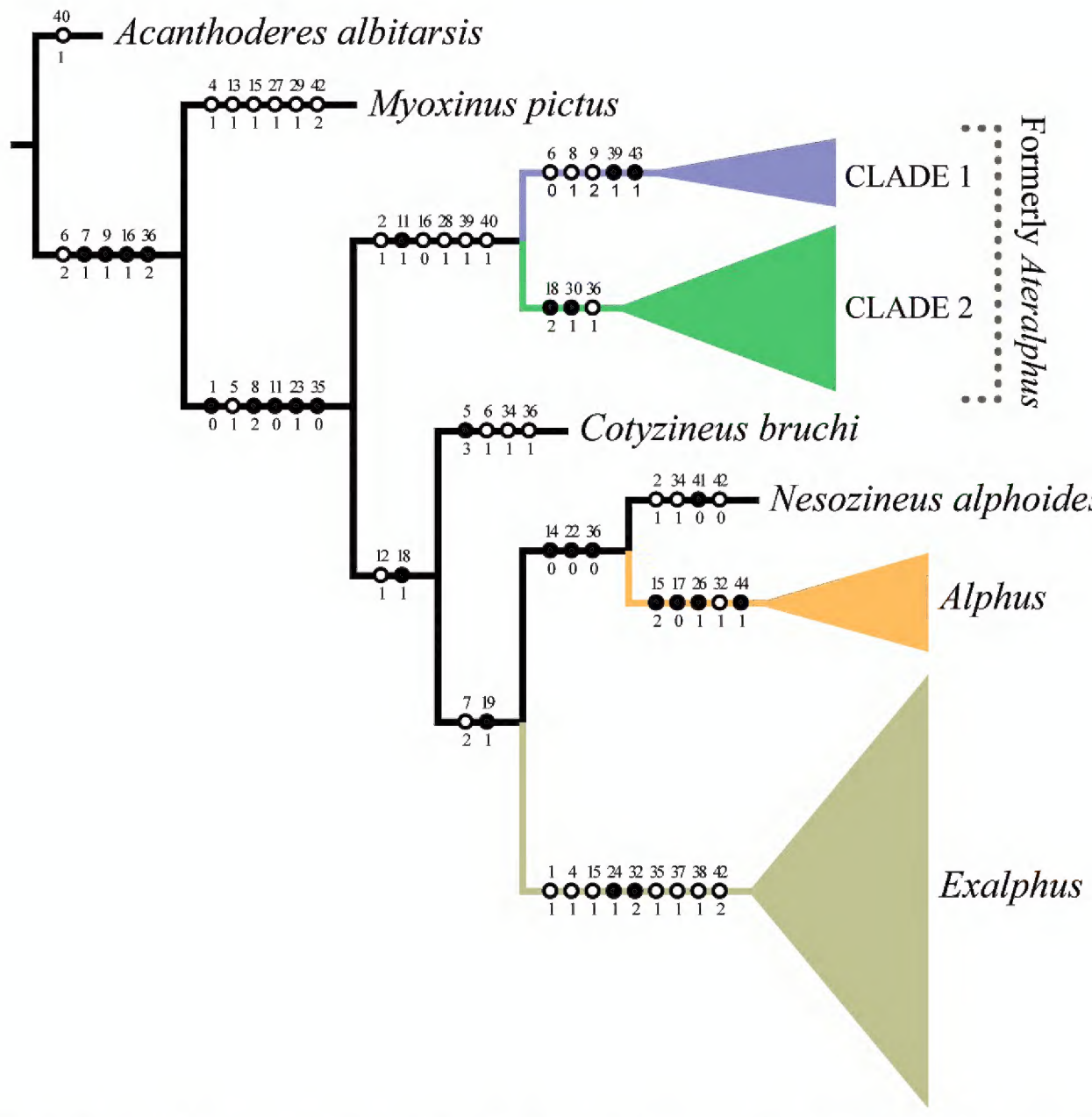


Figure 17. Summarized topology obtained from the cladistics analysis of *Ateralphus* and related genera *Alphus* and *Exalphus*, showing all character state transformations under ACCTRAN optimization. CLADE 1: *Grandateralphus* gen. n.; CLADE 2: Current *Ateralphus*.

1; Fig. 8); and scape gradually expanded toward apex, reaching widest diameter just near apex (9: 2; Fig. 12). Clade 2 includes *A. auritarsus* Souza & Monné, 2013, *A. dejeani*, *A. javariensis* (Lane, 1965), *A. lucianeae* Souza & Monné, 2013, *A. senilis* Bates, 1862 and *A. subsellatus*. This clade was supported by the following character states: post-lateral to median tubercles on the pronotum distinctly raised, appearing as a pair of tubercles (18: 2) and color pattern of the lateral margin of the elytra similar to the rest of the elytra. (30: 1). An additional synapomorphy was obtained under fast optimization for clades 1 and 2, respectively: parameres with setae on apex and inner margin (43: 1); and presence of dark brown setae at apical third (36: 1).

DISCUSSION

Among the genera studied, *Alphus* may be easily recognized by the punctures on the elytra. Restello et al. (2001) cited the arrangement of the punctures on the elytra as one of the most remarkable characteristics that enable the differentiation of *Alphus* from *Ateralphus* and *Exalphus*. In *Alphus*, the elytral punctation is present only on the basal half, arranged in longitudinal rows (Fig. 15), a autapomorphy of the genus in our results. By contrast, in *Ateralphus* and *Exalphus* the elytral punctation is irregularly distributed on the elytra (character 26; Figs 13, 14).

Although the monophyly of *Ateralphus* has been corroborated in this study, we consider that clades 1 and 2 are robust enough (synapomorphic characters, bootstrap and Bremer supports; Fig. 16) to be treated as independent genera. Most character states supporting clade 1 are homoplastic (6: 0; 8: 1 and 9: 2), since they are also observed in *Acanthoderes albitarsis* and in several lineages of *Exalphus*. However, we consider that these character states are important enough to establish the separation of clade 1 from the remaining species of *Ateralphus*. Particularly, we highlight the relevance of characters 6 and 8, which were first used by Souza and Monné (2013b) as key characters to differentiate between the two species groups of *Ateralphus*.

Under ACCTRAN optimization, character state 6: 0 appeared as a plesiomorphic condition, being interpreted here as a reversion in clade 1 (Fig. 17). The transformations of character 8 resulted in a homoplastic synapomorphy for clade 1, with all states widely distributed throughout the topology. The ancestral condition of this character is represented by character state 8: 0 (genae divergent toward apex), whereas character state 8: 1 is an apomorphic condition that appeared independently in several lineages of *Exalphus* and in the representatives of clade 1. As with character 8, character state 9: 2 can also be interpreted as a case of parallelism or convergence since it has two independent origins in our chosen topology. It is a synapomorphy for clade 1 and for the most apical clade of *Exalphus*, which includes *E. lichenophorus*, *E. malleri*, *E. cicatricornis* and *E. calvifrons* (Fig. 16).

In addition to those synapomorphies mentioned above, other characteristics also mentioned by Souza and Monné (2013b) (e.g., shape of the lower ocular lobe, length of antennae and length of the sternite V relative to sternites II, III and IV), are taxonomically important to separate the species of clade 1 from other *Ateralphus*. Thus, considering the taxonomic significance of the characters supporting the clades 1 and 2, we propose splitting *Ateralphus* in two genera: *Ateralphus* (represented by the clade 2), with six species (*A. subsellatus* (type-species of *Ateralphus*), *A. auritarsus*, *A. javariensis*, *A. senilis*, *A. lucianeae* and *A. dejeani*); and *Grandateralphus* gen. n., allocating the species previously grouped in clade 1 (*A. tumidus*, *A. lacteus* and *A. variegatus*). All systematic changes proposed in this study are summarized in the 'TAXONOMY' section below.

Although the monophyly of *Ateralphus*, *Alphus* and *Exalphus* is strongly supported in our analysis, the phylogenetic relationships between them are not well resolved. A single intergeneric clade with bootstrap over 50% (i.e., *Nesozineus alphoides* + *Alphus*) was recovered. It is supported by the following synapomorphies: absence of stain of dark brown setae at apex of antennomeres III to XI (14: 0); mesosternal process slightly convex (22: 0); and, additionally under fast optimization, absence of a stain of dark brown setae on apex of meso- and metatibiae (36: 0).

Despite the low support values, the distribution of the characters on the topology strongly suggests that *Ateralphus* is the sister group of the lineage (*Cotyzineus bruchi* + ((*Nesozineus alphoides* + *Alphus*) + (*Exalphus*)). Supporting this relationship are the following synapomorphies: posterior margin of head triangular (1: 0; Fig. 1B); presence of a row of erect setae reaching basal half of antennal tubercles (5: 1); genae convergent in frontal view (8: 2); mesosternal process 45° angulated at apical third relative to mesosternum (23: 1); and absence of a stain of dark brown setae on half basal region of the meso- and metatibiae (35: 0)). *Myoxinus pictus* has many morphological resemblances with the representatives of *Exalphus* (which is also expressed by the high number of homoplastic characters exclusively shared between *M. pictus* and the *Exalphus* species, i.e., 13: 1; 15: 1; 27: 1 and 29: 1). However, these genera were not recovered as sister groups. Instead, *M. pictus* resulted as a basal lineage (resulting as sister group of all other species included in the analysis), while *Exalphus* was corroborated as sister group of (*Nesozineus alphoides* + *Alphus*), supported by two synapomorphies: lower ocular lobe larger than gena (7: 2); and absence of elevation post-lateral to the median tubercles of the pronotum (19: 1).

After the description of *Alphus*, *Ateralphus* and *Exalphus* by Restello et al. (2001), no other study has treated the relationships among them or between other genera of Acanthoderini. One exception is the discussion of some characters of these genera by Souza and Monné (2013b). Bates (1862) thought that *Alphus* (which at that date also comprised species currently placed in *Ateralphus* and *Exalphus*) was close to *Myoxinus*, comparing and differentiating them from *Acanthoderes* by the shape of the scape, width of the head (measured through the vertex) and shape of

the malar area. In our analysis, such characteristics were adapted and codded in characters 9, 6 and 8, respectively.

Except for *Acanthoderes*, all other species included in our analysis have scape not piriform, slightly shorter than antennomere III (characteristic atypical among the representatives of Acanthoderini). Based mainly on that character, Bates (1862) suggested that *Alphus* was the lineage link between the tribes Acanthoderini and Acanthocinini, the length of the scape being the key character that keeps it within the Acanthoderini, since in Acanthocinini the length of the scape exceeds that of antennomere III. Apart from the shape of the scape, Bates (1862) also pointed out other characteristics that highlight *Alphus* among the Acanthoderini, such as mesosternum narrower toward anterior region, base of coxa angled outward and anterior tarsi of males not dilated.

Considering the insights mentioned by Bates (1862) on the evolution of Acanthoderini and the great number of homoplastic characters in our results due to the morphological plasticity observed among the representatives of the subfamily, we suggest that a more comprehensive phylogenetic study including more representatives of Acanthoderini should be conducted, not only to further explore the relationship between these genera, but also to understand the relationships among the genera of Acanthoderini and to evaluate their tribal classification.

TAXONOMY

Grandateralphus Souza, Monné & Marinoni, gen. n.

http://zoobank.org/82FD03E6-1193-42F5-9A66-D65495D2E0D1

Type-species. *Alphus variegatus* Mendes, 1938.

Description. Frons rectangular; slightly convex, almost flat in lateral view; with a row of long setae near malar area; longitudinal suture well-defined, reaching occiput. Head finely punctate; slightly depressed, with coarse and sparse punctation on vertex; antennal tubercles slightly prominent, obliquely directed. Eyes coarsely faceted. Upper ocular lobes semicircular, bordered at vertex by one row of straight setae; separated by three or more times their width. Lower ocular lobes narrow and rectangular, height less than height of gena. Genae parallel. Labrum covered with dense and short setae; with a transversal row of long setae at median region. Mandibles triangular, symmetrical, apex acuminate; outer margin densely covered with short setae. Scape gradually expanded toward apex, reaching widest diameter near apex; slightly shorter than antennomere III. Pedicel short, gradually expanded toward apex. Antennomeres III–XI with a ring of dark brown setae at apical margin; gradually decreasing in length. Prothorax transverse; coarse and irregularly punctate; covered with short setae; sides with a pointed lateral tubercle. Pronotum straight near anterior margin; disc with a pair of median tubercles and, posterior to these, a small tubercle at midline. Pro-, meso- and metasternum dense and finely punctate. Prosternal process width about 2–3 times narrower than diameter of one procoxa; longitudinally depressed; posterior margin truncate. Mesosternal process straight or tumescent at posterior half; subequal in length to mesocoxa; lateral margins without tubercles; posterior margin bilobed. Elytra completely covered with setae; with coarse punctation irregularly distributed, denser at basal and lateral areas; slightly convex apically; almost straight at basal third; basal-crests raised, with rounded tubercles slightly elevated; from basal-crests, a sinuous carina extending toward apex; with a diagonal carina from humerus to basal-crest carinae. Humeri rounded, slightly projected anteriorly; with small tubercles. Pro- and mesocoxae globular. Femora and tibiae subequal in length. Femora pedunculate. Tibiae gradually enlarged apically; with a spot of dark brown setae at subapical region. Tarsomeres V bicolored, with dark brown setae on apical third or on base and apical third. Abdomen fine and irregularly punctate. Sternite I as long as sternites II, III and IV together; anterior margin long and acuminate; length about two thirds its total length. Sternites II, III and IV subequal in length. Sternite V wider than long; length about equal or less than length of sternites III and IV together; sternite V of females with a median longitudinal sulcus at basal fourth.

Remarks. *Grandateralphus* gen. n. is closely related to *Ateralphus*. Their sister-group relationship is supported by the following synapomorphies: antennomere III subequal to antennomere IV; pronotum straight near anterior margin; and sternite V with longitudinal sulcus at basal region the female abdomen. *Grandateralphus* gen. n. is supported by the following synapomorphies: width of upper ocular lobes less than width between the lobe and the coronal suture (6: 0), genae parallel in frontal view (8: 1) and scape gradually expanded toward apex, reaching widest diameter just near apex (9: 2). In addition to these synapomorphies, *Grandateralphus* gen. n. can be differentiated from *Ateralphus* by the lower ocular lobes rectangular, lesser in height than gena; meso- and metatibiae with a subapical stain of dark brown setae; and sternite V equal or less in length than sternites III and IV together.

Etymology. *Grandateralphus* gen. n. is a combination of the Latin word *grand* (= large) with *Ateralphus*. It is allusive to the size of the representatives of the new genus, which are usually larger in total length than the representatives of *Ateralphus*.

Grandateralphus gen. n. includes the following species (new combinations proposed in this study):

Grandateralphus lacteus (Galileo & Martins, 2006), comb. n.
Grandateralphus tumidus (Souza & Monné, 2013), comb. n.
Grandateralphus variegatus (Mendes, 1938), comb. n.

Taxonomic notes

Taxonomic notes are provided from examination of material belonging to the American Coleoptera Museum, Texas, United States of America (ACMT). Souza and Monné (2013b) registered *G. variegatus* comb. n. (cited as *A. variegatus*) from Bolivia (Santa Cruz) based on primary records in the literature (Wappes et al. 2006). Recently, we had the opportunity

to examine some material from the ACMT and, based on our observations, we exclude the record of *G. variegatus* comb. n. from Bolivia, considering that these records actually correspond to *G. lacteus* comb. n. Also, based on that material, we confirm the literature records of *A. subsellatus* cited by Souza and Monné (2013b) and provide a new country record of *E. cicatricornis* to Bolivia (Santa Cruz).

Material examined. *Grandateralphus lacteus* comb. n. (Galileo & Martins, 2006). Bolivia, Santa Cruz, 4–6 km SSE Buena Vista, F & F Hotel, 1 male, 22–31.x.2002, Wappes and Morris leg.; 1 female, 29–30.x.2003, Robin Clarke leg.; 1 female, 10–15.xi.2003, Robin Clarke leg.; 1 male, 21–24.xi.2003, Wappes, Morris and Nearns leg.; 1 female, 30.ix.2004, Robin Clarke leg.; 1 male, 3–8.x.2004, Wappes and Morris leg.; Reserva Natural Potrrillo del Guenda, Snake Farm, 17°40'26"S, 63°27'43"W, 400 m, 2 males, 2 females, 6–9.x.2006, Wappes, Nearns and Eya leg.; Potrerillo del Guenda, 370 m, 1 female, 16–22.x.2006, Nearns and Eya leg.; Potrerillo del Guenda, Reserva Natural, 40 km Santa Cruz, 17°40'S, 63°27'W, 370 m, 1 male, 16–21.x.2007, F. and J. Romero leg.; Potrerillo del Guenda, Snake Farm, 17°40'S, 63°27'W, 350–400 m, 1 male, 15–22.xi.2011, Bettela, Bonaso and Romero leg.; Potrerillo del Guenda, 17°40'S, 63°27'W, 350–400 m, 1 female, 1.xii.2011, Bettela, Bonaso and Romero leg.; Potrerillo del Guenda, Snake Farm, 17°40'S, 63°27'W, 350–400m, 1 female, 10–18.xii.2011, Bettella, Bonaso and Romero leg.; Potr. Del Guenda, Reserva Natural, Snake Farm, 17°40'15"S, 63°27'26"W, 400 m, 1 male, 1 female, 23–30.x.2013, Wappes and Kuckartz leg.; Potr. Del Guenda, 1 male, 23–30.x.2013, Wappes and Kuckartz leg.; Huaico, Potrerillo, across Guenda fm Potrerillo, 17°40'35"S, 63°26'59"W, 1,270 ft., 1 female, 18.xi.2012, Windsor and Gowin leg.; Huaico, Potrerillo, 17°40'S, 63°26'W, 430m, MV/UV lights, 4 males, 2 females, 27–29.x.2013, Wappes and Kuckartz leg. (ACMT). *Ateralphus subsellatus* (White, 1855). Bolivia, Santa Cruz, Potrerillo del Guenda, Reserva Natural, Snake Farm, 17°40'15"S, 63°27'26"W, 400 m, 1 male, 24–30.x.2012, Betella, Bonaso and Romero leg.; 20 km N Camiri, road to Eyti, 6–8 km E Hwy 9, 19°52'S, 63°29'W, 1250 m, 1 male, 5, 6, 10.xii.2012, Wappes, Bonaso and Skillman leg. (ACMT). *Exalphus cicatricornis* Schmid, 2014. Bolivia, Santa Cruz, Huaico, 17°40'S, 63°24'W, 430 m, 1 female, 21.xi.2013, Skillman and Wappes leg. (ACMT).

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